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Molecular Phylogeny of *Zeylanidium* (Podostemaceae) Showing a New Cryptic Species from Thailand

Masahiro Kato[1] and Satoshi Koi[2,*]

[1] *Department of Botany, National Museum of Nature and Science, Tsukuba 305-0005, Japan;*
[2] *Botanical Gardens, Faculty of Science, Osaka City University, Kisaichi, Katano, Osaka 576-0004, Japan.*
**skoi@sci.osaka-cu.ac.jp (author for correspondence)*

Zeylanidium (Podostemaceae) comprises ribbon-like and crustose-rooted species in Asia, of which *Z. lichenoides sens. lat.* is widely distributed in Sri Lanka, India, Myanmar and Thailand. This study was conducted to clarify its relationships. In the *matK* phylogenetic tree obtained, plants of *Z. lichenoides* from northern Thailand were far from *Z. lichenoides sens. str.* and are separated as a cryptic species, *Z. tailichenoides* sp. nov. *Zeylanidium tailichenoides* is characterized by a 1-locular ovary and is quite similar with *Z. lichenoides sens. lat*. in other characteristics. The remaining *Z. lichenoides sens. lat*. is divided into *Z. lichenoides sens. str.* and three populations that we refer to as *Z. 'lichenoides,'* although morphologically all five are hardly distinguishable. *Zeylanidium tailichenoides* and one population of *Z. 'lichenoides'* are related independently to the crustose species.

Key words: Cryptic species, *matK* phylogeny, paraphyletic species, *Zeylanidium lichenoides*, *Zeylanidium tailichenoides*

The aquatic Podostemaceae are specialized ecologically and morphologically (Cook & Rutishauser 2007, Kato 2013). The plants grow submerged on rocks in the rapids and waterfalls in the tropics and subtropics. They adhere to rock surfaces in the interface between hard rocks and flushing water. The root, a major adhering organ, is subcylindrical, ribbon-like or crustose (foliose). In some species the adhering organs are shoots, basal disks and holdfasts. Those organs adhere with adhesive hairs and a biofilm on the ventral surface.

Podostemaceae comprise about 54 genera, including 22 monotypic genera and 26 genera of 10 or fewer species, i.e., 89% being small genera (Cook & Rutishauser 2007, Koi *et al*. 2012, Kato 2016), indicating that morphological variation between many species are great and abrupt. This has been called saltational evolution (Rutishauser 1997). By contrast, there is little variation even in single species or probably between closely related species. *Tristicha trifaria* (Willd.) Spreng. is exceptionally widely distributed in Africa and America, and varies greatly in molecular sequences (Kita & Kato 2004a). *Dalzellia zeylanica* (Gardner) Wight also has a uniform morphology but great molecular variation (Koi *et al*. 2012). Furthermore, there are several paraphyletic species that are morphologically invariable and include daughter species (Koi *et al*. 2015).

Zeylanidium (Tul.) Engl. is a small genus distributed in India, Sri Lanka, Myanmar and Thailand (van Royen 1965, Cusset 1992). Cusset (1992) recognized four species, *Z. lichenoides* (Kurz) Engl., *Z. olivaceum* (Gardner) Engl., *Z. barberi* (Willis) C. Cusset and *Z. subulatum* (Gardner) C. Cusset. The last two species were excluded from *Zeylanidium* by Mathew & Satheesh (1997). The exclusion of *Z. subulatum* was supported by molecular evidence (Koi *et al.* 2012). *Zeylanidium barberi* is distinct from the others in floral characters (Cusset 1992). Later, *Z.*

maheshwarii C. J. Mathew & Satheesh (Mathew & Satheesh 1997), *Zeylanidium sessile* (Willis) C. D. K. Cook & Rutish. (Cook & Rutishauser 2001), and *Z. crustaceum* M. Kato (Kato *et al*. 2015) were added. Currently, *Zeylanidium* includes five or six species, *Z. crustaceum*, *Z. maheshwarii*, *Z. olivaceum*, *Z. lichenoides*, *Z. sessile* and possibly *Z. barberi*. The first three species have crustose roots with leaves and flowers scattered on the dorsal surface; the last three species have ribbon-like roots with leaves and flowers borne regularly at the sinuses of root branches.

Zeylanidium lichenoides is taxonomically relatively stable and well characterized by vegetative (root, leaf) and reproductive characters (flower, fruit) (Cusset 1992, Kato & Koi 2009). Among its congeners, it is distributed most widely in southern and northeastern India, Sri Lanka, southern Myanmar and northern Thailand (van Royen 1965, Rao & Hajra 1975, Cusset 1992, Kato & Koi 2009). Although infraspecific variation was reported throughout its range of distribution (Willis 1902), it was not formally recognized by Cusset (1992) or Mathew & Satheesh (1997). Recently Koi *et al*. (2012) provided molecular data that *Z. lichenoides* in Thailand is sister to the crustose-rooted *Z. olivaceum/Z. maheshwarii* of southern India and Sri Lanka, while *Z. lichenoides* of southern India belongs to another lineage. These findings support an interpretation that *Z. lichenoides* is apparently paraphyletic or contains cryptic species. Such an interpretation was premature due to scanty samples across the area of distribution, particularly from northeastern India and Myanmar. The phylogenetic relationship of the crustose *Z. crustaceum* was also unknown. To answer these questions, we performed molecular phylogenetic and morphological analyses using additional material from Myanmar and India.

Materials and Methods

Material used in this study was collected in Thailand, Myanmar, India and Sri Lanka (Appendix 1). Material of *Zeylanidium barberi* was not available. The collecting sites of the samples cover most of the area of distribution (Willis 1902, Cusset 1992, Mathew & Satheesh 1997). Specimens *MY-01*, *IND-1502* and *TK-02* were collected at or near the type localities of *Zeylanidium lichenoides* var. *lichenoides*, var. *moosmaiense* Willis and *Z. tailichenoides* sp. nov., respectively (Cusset 1992, present study). *SL-09* was collected not far from the type locality (Sri Lanka) of *Z. olivaceum*. Vouchers are deposited in the Herbarium, Department of Botany, National Museum of Nature and Science (TNS), the Forest Herbarium, Department of National Parks, Wildlife and Plant Conservation, Bangkok (BKF), the University of Calicut Herbarium (CALI), and the University of Tokyo Herbarium (TI).

The methods of DNA extraction, PCR amplification of the chloroplast *matK* gene (1,530–1,596 bp) and sequencing were employed following Koi *et al*. (2012).

The sequences obtained in this study and those deposited in GenBank were used for phylogenetic analysis (Appendix 1). The sequences were aligned by CLUSTAL X (Thompson *et al*. 1997) and refined manually with MacClade 4.0 (Maddison & Maddison 2000). Gaps were treated as missing data. The program MrModeltest 2.3 (Nylander 2004) determined a general time reversible (GTR) + G (shape parameter of the gamma distribution) + I (proportion of invariable sites) substitution model as the best fitting model of substitution: nucleotide frequencies were A = 0.3320, C = 0.1496, G = 0.1326, T = 0.3858; the substitution rate matrix was A to C = 0.9481, A to G = 1.1018, A to T = 0.1215, C to G = 0.2571, C to T = 0.7550, G to T = 1.0000; the proportion of invariable sites was 0.4628; and the gamma distribution shape parameter was 0.9746. Maximum likelihood (ML) and maximum parsimony (MP) analyses were conducted using the program PAUP* 4.0b10 (Swofford 2002). In maximum likelihood (ML) analysis, heuristic searches were conducted with 100 random addition replicates involving nearest-neighbor-interchange (NNI) branch swapping. Bootstrap values were calculated for 100 replicates with 10 random addition rep-

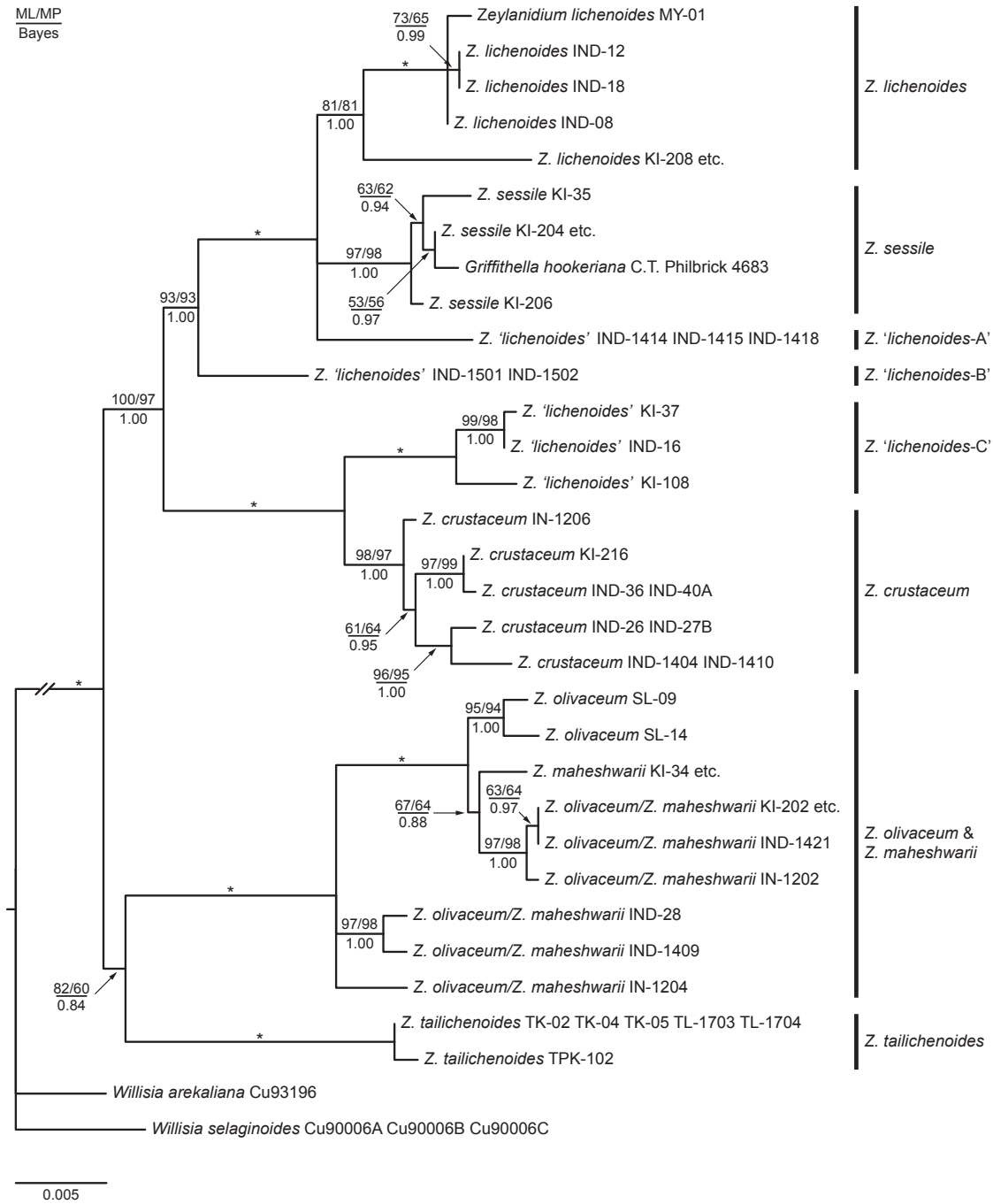

FIG. 1. ML phylogenetic tree deduced from *matK* sequences. Numbers above and below branches are bootstrap values (%) of ML (left) and MP (right) and Bayesian posterior probabilities, respectively. Asterisks indicate branches supported with 100% ML and MP bootstrap values and 1.00 Bayesian posterior probability. *Willisia* species are outgroups. Clades found in this study are shown on the right side. '*Z. lichenoides* KI-208 etc.' consists of *KI-208*, *Cu-90093*, *IND-22* and *IN-1208*; '*Z. sessile* KI-204 etc.' consists of *Z. sessile KI-204*, *KI-207*, *Cu90094A*, *IND-23*, *IND-1403* and *IN-1210*; '*Z. olivaceum/Z. maheshwarii* KI-202 etc.' consists of *Z. olivaceum/Z. maheshwarii KI-202*, *Cu90092B* and *Cu90092C-2*; and '*Z. maheshwarii* KI-34 etc.' consists of *Z. maheshwarii KI-34*, *IND-09*, *IND-11*, *IND-15* and *IND-17.*

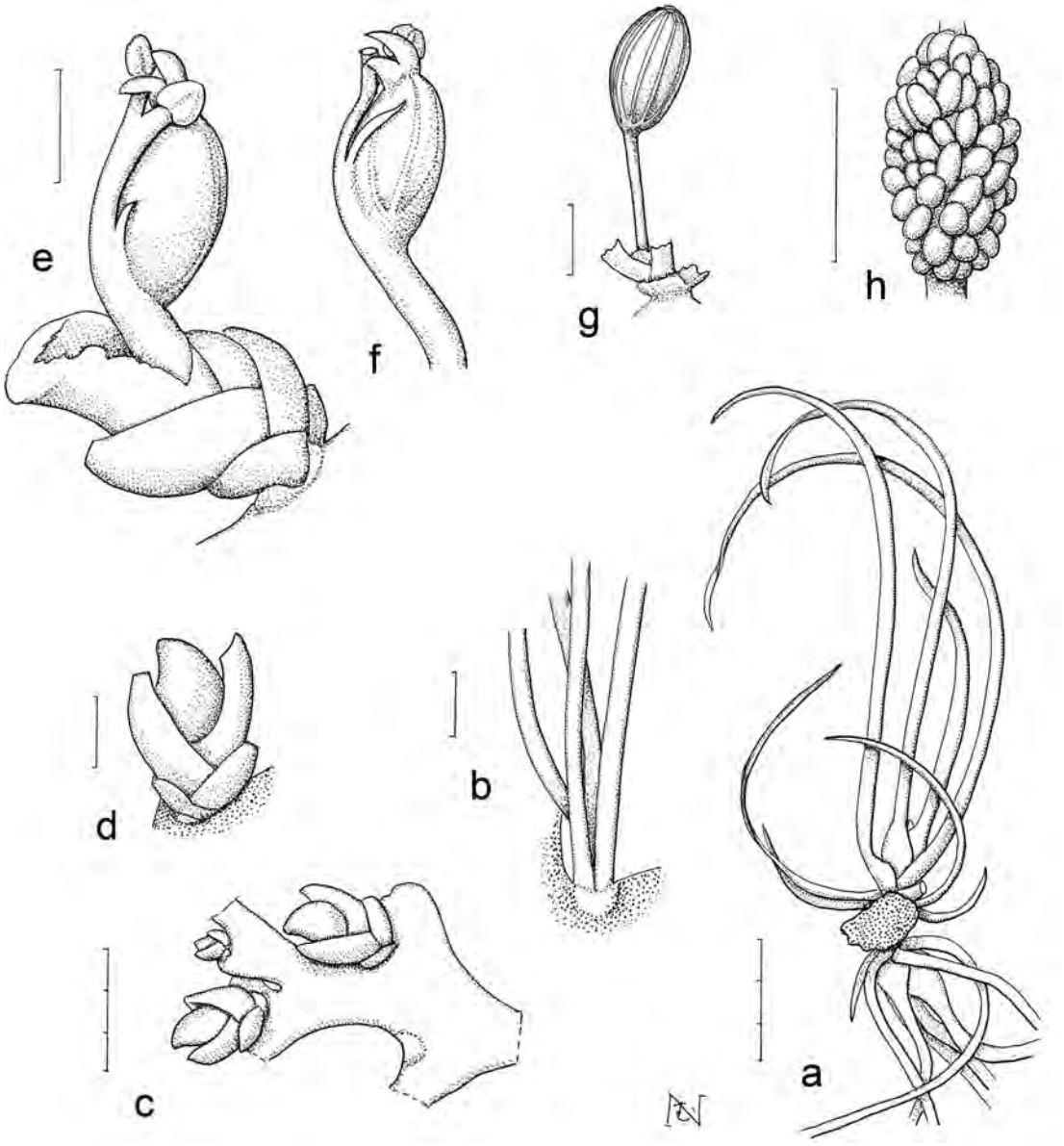

FIG. 2. *Zeylanidium tailichenoides*: *S. Koi & T. Wongprasert TK-02*: **a**. Tufts of leaves on root segment; ventral view. **b**. Tuft of leaves in sinus of root. **c**. Flower buds in sinuses of root branches. **d**. Flower bud enclosed by spathella subtended by bracts. **e**. Flower extruding from ruptured spathella subtended by bracts. **f**. Older flower. **g**. Fruit. **h**. Ovules on placenta free along margins. Scale bars = 3 mm in **a** & **c**, 1 mm in **b**, **d**, **e**, **g** & **h**.

licates involving NNI branch swapping. In maximum parsimony (MP) analyses, all characters were equally weighted, and heuristic searches were conducted with 1,000 random addition replicates involving tree-bisection-reconnection (TBR) branch swapping. Strict consensus tree was built with the best-scored trees obtained. Bootstrap values were calculated for 1,000 replicates with 100 random addition replicates involving TBR branch swapping. In the Bayesian analysis, Markov chain Monte Carlo (MCMC) iterations with four chains were conducted under the

GTR + G + I model for 2,000,000 generations, sampling a tree every 100 generations, with the program MrBayes 3.2.5 (Ronquist *et al*. 2012). Potential scale reduction factors (PSRF) of all parameter approached 1.000 as runs converge. The first 5,000 trees were discarded as burn-in and the remaining 15,000 trees were used to determine the posterior probabilities for branches. Species of *Willisia* were treated as outgroup.

Results

The trees obtained in the ML and Bayesian analyses, and the consensus tree obtained from nine best-scored trees in the MP analysis showed the same phylogenetic topology among the species (Fig. 1; the Bayesian and MP trees are not shown). In the molecular phylogenetic tree obtained, the monophyly of the *Zeylanidium lichenoides* lineage including *Z. crustaceum*, *Z. lichenoides*, *Z. olivaceum*, *Z. maheshwarii* and *Z. sessile* was robustly supported (Fig. 1). The lineage was divided into four clades. One clade from northeastern India was subdivided into *Z. 'lichenoides*-B,*'* and the rest, which included Z. *lichenoides sens. str.* (specimen *MY-01* from southern Myanmar and specimens from southern India), *Z. sessile* and *Z. 'lichenoides*-A*'* from southern India. The second clade was divided into *Z. 'lichenoides*-C*'* and *Z. crustaceum*, both from southern India. The third clade comprised *Z. olivaceum* and *Z. maheshwarii* from southern India and Sri Lanka, and the fourth clade comprised *Z. lichenoides* of Thailand.

Morphological comparison of *Z. lichenoides sens. lat.* using specimens from northeastern India, southern Myanmar, northern Thailand (Kato & Koi 2009), southern India, and Sri Lanka found that there was little difference among the specimens in both vegetative and reproductive characteristics, i.e., the width of the roots (1–4 mm), the tufted leaves and floriferous shoots borne regularly in sinuses of the root branches, several bracts with linear distal parts, flowers with two tepals, two stamens with a common andropod, ellipsoid ovary, two narrowly deltoid stigmas, short stalk (1–3 mm) of the capsule, 8-ribbed, sessile or subsessile capsules. The Thai specimens differed from the rest, including those from southern Myanmar and northeastern India, in the anatomy of the ovary; 1-locular in the former and 2-locular in the latter.

Discussion

Zeylanidium lichenoides has been treated in a broad sense based on morphology (Willis 1902, van Royen 1965, Rao & Hajra 1975, Cusset 1992, Mathew & Satheesh 1997, Kato & Koi 2009). Results of the phylogenetic analysis indicate that *Z. lichenoides* of Thailand is separated from all other congeners. It is discriminated as an independent species only by the anatomy of the ovary, but not by any other vegetative or reproductive characteristics. We also found that specimen *MY-01* of Myanmar collected at/near the type locality of *Z. lichenoides* forms a monophyletic clade with the southern Indian plants. *Zeylanidium lichenoides sens. str.* should therefore exclude the Thai plants.

Our morphological observations showed that *Z. lichenoides sens. lat*., excluding plants from Thailand, varies little: the root is ribbon-like with tufts of leaves and floriferous shoots in sinuses of branches, the distal part of the bract is linear, the two stamens have a common andropod, the stigmas are narrowly deltoid, and the ovary/capsule is short-stalked, 2-locular, 8-ribbed and usually ellipsoid (see Key below). By contrast, the molecular data showed that *Z. lichenoides sens. lat.* is divisible into four clades (*Z. lichenoides sens. str.* and three additional clades collectively called *Z. 'lichenoides'*). *Zeylanidium lichenoides* and '*lichenoides*-A' are close to *Z. sessile*, and *Z. 'lichenoides*-C*'* is sister to *Z. crustaceum*. It may indicate that *Z. lichenoides* and *Z. 'lichenoides'* are one paraphyletic species that produced daughter species, or that it represents multiple morphologically inseparable species. *Zeylanidium lichenoides sensu* Cusset (1992) included several species and varieties described from northeastern and southern India and Sri Lanka. Specimen

IND-1502 of *Zeylanidium 'lichenoides*-B*'* was collected from Mawsmai waterfall, Cherrapunji, northeastern India, where *Z. lichenoides* var. *moosmaiensis* Willis was described. This variety may be recognized as a species in a future study. Investigation of the previously proposed local species and varieties is necessary to clarify the taxonomy and phylogeny of *Z. lichenoides sens. lat*.

Zeylanidium lichenoides sens. str., *Z. 'lichenoides'* and *Z. tailichenoides* are distributed in southern India, Sri Lanka, northeastern India, southern Myanmar and northern Thailand; the first two are geographically distant from the last three. *Zeylanidium lichenoides sens. str.* is distributed in Myanmar and southern India, and is phylogenetically close to southern Indian *Z. 'lichenoides*-A*'* and *Z. sessile* (Fig. 1). Northeastern Indian *Z. 'lichenoides*-B*'* is related to the southern Indian lineages. *Zeylanidium tailichenoides*, restricted to northern Thailand, is sister to the southern Indo–Sri Lankan *Z. olivaceum–Z. maheshwarii*. Since the three species of northeastern India, southern Myanmar and northern Thailand are phylogenetically not related to each other, and most species in the *Zeylanidium* clade are distributed in southern India, the distribution of the three species was likely established by long distance dispersal events from southern India. However, it remains uncertain what factor caused the establishment of such a distribution pattern.

Our phylogenetic results show that *Zeylanidium sessile* is close to *Z. lichenoides* and *Z. 'lichenoides*-A,*'* and are consistent with Cook & Rutishauser's (2001) taxonomic transfer from *Hydrobryopsis*. *Zeylanidium sessilis* is characterized by slightly wider (2.5–4 mm *versus* to 2 mm in *Z. lichenoides*) ribbon-like roots, two stamens, and sessile or short stalked (to 1.2 mm *versus* to 2 mm), globose-obovoid, smooth-surfaced capsules (*versus* ellipsoid, ribbed). Because of the subtle differences in these characters, it is suggested that *Z. sessile* is a local species derived from the *Z. lichenoides-Z. 'lichenoides'* lineage.

In *Zeylanidium*, three species, *Z. crustaceum*, *Z. olivaceum* and *Z. maheshwarii*, have crustose roots with tufts of leaves and floriferous shoots scattered on the dorsal surface. However, *Z. crustaceum* differs from the other two in the floral and fruit organs (Kato *et al*. 2015); and *Z. olivaceum* is unique in having long hypocotyls (Suzuki *et al*. 2002). Our phylogenetic data indicate that the two clades are sister to *Z. 'lichenoides'* and to *Z. tailichenoides*, respectively, which suggests that divergence between crustose and ribbon-like roots happened in two lineages. It is equivocal whether ribbon-like roots are derived from crustose roots or *vice versa* (data not shown). Hiyama *et al*. (2002) showed different modes of root development. In ribbon-like roots the root meristem is split by the leaf primordia that are produced within the meristem, while the meristem of the crustose root is continuously marginal and is not split by the leaf primordia, because the leaf primordia form proximal to the meristem. Hiyama *et al.* (2002) suggested that crustose roots were derived from ribbon-like roots by an inward shift of the initiation site of the leaf primordia. Since crustose roots appear to be a characteristic adaptation for Podostemaceae (Cook & Rutishauser 2007, Kato 2013), the evolutionary trend in root morphology is an interesting issue.

Description of New Species

Zeylanidium tailichenoides M. Kato & Koi, **sp. nov.** —Fig. 2

Different from *Zeylanidium lichenoides* in the 1-locular ovary, but hardly separable from it in the width of ribbon-like roots, length of the stamens, the pedicellate ellipsoid ovary, narrowly deltoid stigmas and the 8-ribbed capsules. Phylogenetically it is sister to the crustose-rooted *Z. olivaceum* and *Z. maheshwarii* and far from any plants of *Z. lichenoides* and *Z. 'lichenoides'*.

Typus. Northern Thailand. Chiang Mai province: Huay Kaew stream, Maetakhrai National Park, Mae On, 18°51'49" N, 99°28'12" E, 600 m alt., Dec. 16, 2008, *S. Koi & T. Wongprasert TK-02* (holo- BKF; iso- TNS).

Roots ribbon-like, 1–2 mm wide, branched; tufts of leaves or floriferous shoots borne in sinuses of root branches; leaves linear, 20–30 mm long, ensiform, ca. 5 per tuft in 2 files. Floriferous shoots soli-

tary, appressed; bracts 4 or 5, in 2 files, uniform but basal ones smallest; basal bracts ovate to ovate-lanceolate, 0.8–1.5 mm long; distal bracts linear, 5–7 mm long, caducous; spathellas ellipsoid, 1.2–1.8 mm long, rupturing longitudinally, persistent: flowers erect; pedicels horizontal at base, distally upright, 1.2–1.5 mm long; tepals 2, on each side of stamen, filiform, 0.5–0.8 mm long; stamens 2, with flattened andropod, branched 1/3–1/4 from apex, 1.8–2 mm long, as long as pistil; anthers ellipsoid, ca. 0.5 mm long; ovary solitary, ellipsoid, 1.2–1.8 mm long, ca. 1 mm in diam., sessile, 1-locular; stigmas 2, forked above or at base, equal, narrowly triangular, ca. 0.5 mm long; ovules 82–115 per ovary, born on whole surface of free septum; capsule stalked (stalk 1.6–2 mm long), ellipsoid, ca. 1.5 mm long, ca. 1 mm in diam., 8-ribbed, dehiscing by 2 unequal valves.

Distribution. Northern Thailand. Chiang Mai province: May On, Doi Suthep (van Royen 1965), Doi Inthanon (van Royen 1965), altitude 600–700 m.

Notes. *Zeylanidium tailichenoides* is the only species of *Zeylanidium* in Thailand. In previous morphology-based floristic work, it was identified as *Zeylanidium lichenoides* (van Royen 1965, Kato & Koi 2009). *Zeylanidium tailichenoides* occurs only at a few spots in Chiang Mai, northern Thailand. It is not closely related to *Z. lichenoides sens. str.* of southern Myanmar and *Z. 'lichenoides'* of north-eastern India, but may be related to the crustose-rooted *Z. olivaceum* and *Z. maheshwarii* of southern India and Sri Lanka.

Other specimens examined. Huay Kaew stream, Maetakhrai National Park, Mae On, *S. Koi & T. Wongprasert TK-02* (TNS), *TK-04* (TNS), *TK-05* (TNS); *ibid*., 18°51'51" N, 99°17'31" E, 650 m alt., *M. Kato*, *C. Tsutsumi*, *Y. Hirayama*, *N. Katayama* & *T. Wongprasert TL-1703*(TNS), *TL-1704* (TNS).

Key to the species of *Zeylanidium*

1a. Root ribbon-like; tufts of leaves and floriferous shoots borne in every sinus of root branches. 2
1b. Root crustaceous; tufts of leaves and floriferous shoots scattered on dorsal surface of roots. 4
2a. Capsules sessile or short stalked (stalk to 1.2 mm long), globose or obovoid, surface smooth ..... *Zeylanidium sessile*
2b. Capsules stalked (stalk 14 mm long), ellipsoid, rarely obovoid, 8-ribbed, ribs rarely obscure. 3
3a. Ovary 2-locular ..... *Zeylanidium lichenoides* and *Z. 'lichenoides'*
3b. Ovary 1-locular ..... *Zeylanidium tailichenoides*
4a. Stigmas subulate ..... *Zeylanidium crustaceum*
4b. Stigmas multilobed or serrate. 5
5a. Stigmas 2-lobed, lobes serrate, long stem (hypocotyl) with leaves at apex on root ..... *Zeylanidium olivaceum*
5b. Stigmas multilobed, long stem absent ..... *Zeylanidium maheshwarii*

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APPENDIX 1. Materials used in this study. Species names are followed by location, date, voucher and GenBank accession number (in parentheses).

Zeylanidium lichenoides. India. Karnataka state: Hebbe Waterfall, Chikmagalur, Kemmanagundi, *C. Tsutsmi & M. Kato IND-08* (LC269059) (TNS). Kerala state: *M. Kato & N. Katayama KI-208* (AB698431*) (TNS); *A. K. Pradeep Cu-90001* (AB698429*) (TNS); Thippalikkyayam, Mangalan Dam, Palakkad, *Manudev & A. K. Pradeep Cu-90093* (LC269060) (TNS); Mangalam Dam, Palakkad, *M. Kato IN-1208* (LC269061) (TNS); Soochipara Waterfall, Wayanad, *C. Tsutsmi & M. Kato IND-12* (LC269062) (TNS); Kanthanpara Waterfall, Wayanad, *C. Tsutsmi & M. Kato IND-18* (LC269063) (TNS); Kanthanpara Waterfall, Thippalikayam near Alugalchattam 13 km from Mangalam Dam, Palakkad, *C. Tsutsumi & M. Kato IND-22* (LC269064) (TNS). Myanmar. Mon state: Ban Bauy Gone Village, Mottama, *M. Kato MY-01* (LC269058) (TNS).

Zeylanidium sessile. India. Kerala state: Thippalikkyayam, Mangalan Dam, Palakkad, *A. K. Pradeep Cu-90094* (LC269065) (TNS); Mangalam Dam, Palakkad, *M. Kato IN-1210* (LC269066) (TNS); Kanthanpara Waterfall, Thippalikayam near Alugalchattam 13 km from Mangalam Dam, Palakkad, *C. Tsutsumi & M. Kato IND-23* (LC269067) (TNS); Thippalikayam near Alugalchattam 13 km from Mangalam Dam, Palakkad, *S. Koi & M. Kato IND-1403* (LC269068) (TNS); *M. Kato & R. Imaichi KI-35* (AB048828**) (TNS); *M. Kato & S. Koi KI-119* (AB698237*) (TNS); *M. Kato & N. Katayama KI-204* (AB698238*) (TNS); *M. Kato & N. Katayama KI-206* (AB698239*) (TNS); *M. Kato & N. Katayama KI-207* (AB698240*) (TNS); *C. T. Philbrick 4683* (HQ331612) [as *Griffithella* hookeriana (Ruhfel *et al*. 2011)].

***Zeylanidium 'lichenoides*-A'.** India. Kerala state: Meenmutty Waterfall, Thiruvananthapuram, S. *Koi & M. Kato IND-1414* (LC269069) (TNS); *ibid., S. Koi & M. Kato IND-1415* (LC269070) (TNS); Kaalakkayam Waterfall, Thiruvananthapuram, *S. Koi & M. Kato IND-1418* (LC269071) (TNS).

***Zeylanidium 'lichenoides*-B'.** India. Meghalaya state: Umtingar, *M. Kato IND-1501* (LC269072) (TNS); Mawsmai Waterfall, Cherrapunji, M. Kato IND-1502 (LC269073) (TNS).

Zeylanidium 'lichenoides*-C'.** India. Kerala state: Kanthanpara Waterfall, Wayanad, *C. Tsutsumi & M. Kato IND-16* (LC269074) (TNS); *C. Tsutsumi & M. Kato KI-37* (AB104582) (TNS); *C. Tsutsumi & M. Kato KI-108* (AB698423*) (TNS).

Zeylanidium crustaceum. India. Kerala state: Verala, Idduki, *M. Kato IN-1206* (LC269075) (TNS); Athirappilly Waterfall, Thrissur, *C. Tsutsumi & M. Kato IND-26* (LC269076) (TNS); ibid., *C. Tsutsumi & M. Kato IND-27B* (LC269077) (TNS); Pooyamkutti, Ernakulam, *C. Tsutsumi & M. Kato IND-36* (LC269078) (TNS); ibid., *C. Tsutsumi & M. Kato IND-40A* (LC269079) (TNS); Padagiri, SW of Nalliyampathy, Palakkad, *S. Koi & M. Kato IND-1404* (LC269080) (TNS) (TNS); Padagiri, SW of Nalliyampathy, Palakkad, *S. Koi & M. Kato IND-1410* (LC269081) (TNS); *M. Kato & N. Katayama KI-216* (AB698432*) (TNS).

Zeylanidium olivaceum. SRI LANKA: *M. Kato et al. SL-09* (AB038207**); *M. Kato et al. SL-14* (AB104581***) (TNS).

Zeylanidium maheshwarii. India. Karnataka state: Hebbe Waterfall, Kemmanagundi, Chikmagalur, C. Tsutsumi & M. Kato IND-09 (LC269082) (TNS). Kerala state: *M. Kato & R. Imaichi KI-34* (AB048379**) (TNS); Soochipara Waterfall, Wayanad district, *C. Tsutsumi & M. Kato IND-11* (LC269083) (TNS); Kanthanpara Waterfall, Wayanad district, *C. Tsutsumi & M. Kato IND-15* (LC269084) (TNS); ibid., *C. Tsutsumi & M. Kato IND-17* (LC269085) (TNS).

Zeylanidium olivaceum/Z. maheshwarii. India. Kerala state: Mangalan Dam, Thippalikkayam, Palakkad, *A. K. Pradeep Cu-90092B* (LC269086) (TNS); ibid., *A. K. Pradeep Cu-90092C* (LC269087) (TNS); Idduki, *M. Kato IN-1202* (LC269088) (TNS); Verala near Irumpupalam and Adimali, Idukki, *M. Kato IN-1204* (LC269089) (TNS); Stream near Vazhachal Waterfall, Thrissur district, *C. Tsutsumi & M. Kato IND-28* (LC269090) (TNS); Padagiri, SW of Nalliyampathy, Palakkad, *M. Kato IND-1409* (LC269091) (TNS); Thippalikayam near Alugalchattam 13 km from Mangalam Dam, Palakkad district, *S. Koi & M. Kato IND-1421* (LC269092) (TNS); *M. Kato & N. Katayama KI-202* (AB698430*) (TNS).

Zeylanidium tailichenoides. Thailand. Chiang Mai prov.: *S. Koi & T. Wongprasert TK-02* (AB698424*) (TNS); *S. Koi & T. Wongprasert TK-04* (AB698425*) (TNS); *S. Koi & T. Wongprasert TK-05* (AB698426*) (TNS); *M. Kato et al. TL-1703* (AB698427*) (TNS); *M. Kato et al. TL-1704* (AB698428*) (TNS); Mae Lai stream, Than Tong village, *S. Koi & P. Werukamkul TPK-102* (LC269093) (TNS).

Willisia arekaliana. INDIA. Kerala state: *A. K. Pradeep Cu-93196* (AB698418*) (TNS).

Willisia selaginoides. INDIA. Kerala state: A. K. Pradeep Cu-90006A (AB698419*) (TNS); *A. K. Pradeep Cu-90006*B (AB698420*) (TNS); *A. K. Pradeep Cu-90006*C (AB698421*) (TNS).

* Koi *et al.* (2012); ** Kita & Kato (2001); *** Kita & Kato (2004b).